The forerunners of this resurgence of interest in the relationships between the Apocynaceae and the Asclepiadaceae were two papers, neither of which was focused on the Apocynaceae s.l., but both of which contained a cladistic analysis of Apocynaceae and Asclepiadaceae based on morphological characters. Both papers included only nine ingroup taxa, together with Loganiaceae/Gentianaceae or Loganiaceae alone as the outgroup. The earlier of the two, by Wanntorp (1988), pointed out that Apocynaceae s. str. are paraphyletic, and thus proposed inclusion of Asclepiadaceae within Apocynaceae. In addition, it questioned Schumann's (1895) interpretation of pollinium orientation in Asclepiadaceae, underscoring doubts raised earlier by Demeter (1922) and Safwat (1962). Schumann (1895) considered the taxa with pendent pollinia (the Asclepiadeae) to be the most primitive in the Asclepiadoideae, and those with erect pollinia as the "crowning glory" of the entire family. In contrast, in Wanntorp's (1988) analysis, the Asclepiadeae came out as the crown clade, suggesting that erect orientation of pollinia is ancestral, rather than derived, and that pendent orientation is an apomorphy of the Asclepiadeae, making them the most derived tribe of the asclepiads. This position is supported in the contribution by Liede (2001) in this volume.

The second paper, by Judd et al. (1994), also recognized that the Apocynaceae s. str. are paraphyletic and proposed amalgamation of Apocynaceae and Asclepiadaceae in order to make the group monophyletic. In addition, this was the first paper to suggest that the congenitally syncarpous ovary in Carissa may not be the ancestral condition in the family, as had been proposed in all traditional classifications (e.g., Schumann, 1895; Leeuwenberg, 1994). This hypothesis was confirmed for Acokanthera two years later based on molecular (Sennblad & Bremer, 1996) as well as combined morphological and molecular (Endress et al., 1996) data.

The first important paper contributing toward the rebirth of the Apocynaceae s.l., and dealing explicitly with the family, was that by Sennblad and Bremer (1996), which was based on sequence data of the rbcL gene for 24 taxa of Apocynaceae s.l. The results of this study indicated that the Asclepiadaceae are nested within the Apocynaceae. Recognition of Asclepiadaceae as a separate family would result in a paraphyletic Apocynaceae. Further, even monophyly of the traditional Asclepiadaceae was questioned, since Parquetina (= Periploca) (Periplocoideae) came out as sister to Prestonia (Apocynoideae). The authors recommended the amalgamation of the two families. In addition, weaknesses in the traditional classification of Apocynaceae s. str. were indicated. One of the most notable results was the position of Alstonia, as the basalmost taxon in the Apocynaceae, which was the first well-supported crack in the veneer of the traditional classifications of Apocynaceae s. str., all of which considered the syncarpous Carisseae to be at the base of the family. Acokanthera and Picralima (both Carisseae in traditional classifications), on the other hand, came out significantly higher on the tree.

Swarupanandan et al., also in 1996, published a classification, which incorporated new morphological characters, such as whether there was a distinct style between the ovaries and the stylehead, and the location of attachment of pollinia to caudicles (rather than the orientation of the pollinia, as in earlier classifications). They proposed a controversial new subdivision of the Asclepiadaceae, which recognized three tribes: Secamoneae, Stapelieae (= Ceropegieae), and Asclepiadeae. Marsdenieae were included in Stapelieae, and Gonolobeae were included in Asclepiadeae. Periplocoideae were excluded from Asclepiadaceae and treated as a separate family. Most subsequent analyses support the inclusion of Gonolobeae in Asclepiadeae and do not refute including Marsdenieae in Ceropegieae, whereas the relationships of Periplocoideae remain unresolved.

The next paper to suggest that all was not rosy in the traditional classifications of Apocynaceae s. str. was that by Endress et al. (1996), which was a combined analysis including rbcL and matK sequences, as well as 48 morphological characters for 14 genera of Apocynaceae s. str. and several outgroup genera from various families of the Gentianales. The results of this study agreed overall with those of Sennblad and Bremer (1996).

In 1998 Sennblad et al. published a paper focused on the Wrightieae (sensu Leeuwenberg, 1994), in which sequence data of the rbcL gene and 25 morphological characters for 21 taxa of Apocynaceae s.l. were cladistically analyzed. The results suggested that in the classification of Apocynaceae s. str. by Leeuwenberg (1994), not only are the Wrightieae and its subtribes paraphyletic, but so are all of the other tribes of higher Apocynoideae. As in their previous paper (Sennblad & Bremer, 1996), Periploca grouped with taxa of the Apocynoideae, rather than with Secamone (Asclepiadaceae). Perhaps most surprising of all was the position of Baissea (Apocynoideae) as a sister group to Secamone.

Focusing on the basal clades of the former Asclepiadaceae, Civeyrel et al. (1998) studied 46 taxa using the gene matK, and then compared the phylogeny obtained with palynological characters that have traditionally been used to delimit subfamilies and tribes. In this phylogeny Asclepiadaceae (including Periplocoideae, Secamonoideae, and Asclepiadoideae) were monophyletic. However, none of the crucial taxa of the higher Apocynoideae were included, thus reducing the significance of this analysis as to predicting whether or not the traditional Asclepiadaceae are monophyletic. Within the Asclepiadoideae, Fockea was found to be sister to the rest of the Asclepiadoideae, supporting recognition of Fockeeae as a separate tribe of Asclepiadoideae, as had been proposed previously by Kunze et al. (1994) based on morphological evidence. The analysis also showed that parallelisms have occurred in a number of the palynological characters traditionally used to delimit tribes.

In 2000 Sennblad and Bremer expanded their original rbcL-based study from 1996 to include 77 taxa of Apocynaceae s.l. The results were very similar to their previous rbcL analysis. The six included taxa of Periplocoideae formed a clade with the three taxa of the Echiteae (higher Apocynoideae), whereas Baissea (higher Apocynoideae) was intercalated between Secamonoideae and Asclepiadoideae. Cibirhiza (the other genus of Fockeeae) came out as sister to the rest of the Asclepiadoideae, providing additional support for recognition of the tribe Fockeeae.

Most recently, Liede and coworkers (e.g., Liede, 2001; Liede & Täuber, 2000; Liede et al., in press) have focused on the subtribal classification within the large tribe Asclepiadeae, which, judging by the results of these papers, is also sorely in need of revision.

It seems clear now that the Apocynaceae and Asclepiadaceae are best united into a single family. Repeatedly, morphological characters assumed to be stable have turned out to be parallelisms, with the result that long-standing taxa are no longer valid, or traditionally recognized taxa have been found to be grades rather than clades (Goyder, 1999). A new classification of Apocynaceae s.l. was recently published by Endress and Bruyns (2000), which recognized five subfamilies: Rauvolfioideae, Apocynoideae, Periplocoideae, Secamonoideae, and Asclepiadoideae. The delimitation and relationships among the tribes therein are still unresolved, as is the position of Periplocoideae (i.e., the question of monophyly of Asclepiadaceae).

The 16th International Botanical Congress held in August of 1999 in St. Louis, Missouri, was thus an opportune time for a symposium on Apocynaceae s.l., in which systematists, employing various disciplines and working on different subfamilies or tribes or with taxa from different geographic regions, could come together and present their results and exchange ideas. The goals were to achieve a better understanding of the evolution of these highly specialized flowers and to develop a more collaborative effort toward a consensus classification of the group.

Progress has been made in our efforts to come up with a consensus classification. Most specialists in the family now accept the five subfamilies given in Endress and Bruyns (2000): Rauvolfioideae, Apocynoideae, Periplocoideae, Secamonoideae, and Asclepiadoideae. We are aware that the first two subfamilies are paraphyletic, but until more data are available, recognition of these two subfamilies seems to be the most prudent avenue to follow. Based on the analyses presented in this volume, the Secamonoideae could also be interpreted as a tribe of the Asclepiadoideae. However, the Secamonoideae are characterized by a number of distinctive morphological characters, and it might be rash to reduce them to a tribe until more information is available. Tribal delimitation is more problematic, especially in the two basalmost subfamilies, Rauvolfioideae and Apocynoideae. The tribes presented in Endress and Bruyns (2000) for these two basalmost subfamilies (nine tribes in Rauvolfioideae and five tribes in Apocynoideae) are currently the best that we have. Both Periplocoideae and Secamonoideae are probably best left without delimitation into tribes at present. Asclepiadoideae, which are by far the largest subfamily, are considered to comprise four tribes: Fockeeae, Marsdenieae, Ceropegieae, and Asclepiadeae (including Gonolobeae). Although the two genera of the Fockeeae (Cibirhiza and Fockea) were included in Marsdenieae by Endress and Bruyns (2000), recognition of Fockeeae as their own tribe is supported in all analyses of asclepiads presented in this volume. Other interpretations of tree topologies within the Asclepiadoideae could be the inclusion of the Marsdenieae in the Ceropegieae (as proposed by Swarupanandan et al., 1996). Conversely, the Gonolobeae could be reinstated as a separate tribe. Below the tribal level the situation is far too nebulous to attempt to provide a unified classification, though Liede continues to work on the relationships in the large tribe Asclepiadeae (Liede, 2001; Liede & Täuber, 2000; Liede et al., in press).

The seven papers that follow are the result of the symposium, entitled "Evolution and Phylogenetics

of the Apocynaceae s.l." In these papers, subfamilies and tribes follow this classification outline:

RAUVOLFIOIDEAE Kostel.
 Alstonieae G. Don
 Vinceae Duby
 Willughbeieae A. DC.
 Tabernaemontaneae G. Don
 Melodineae G. Don
 Hunterieae Miers
 Plumerieae E. Mey.
 Carisseae Dumort.
 Alyxieae G. Don
APOCYNOIDEAE Burnett
 Wrightieae G. Don
 Malouetieae Müll.-Arg.
 Apocyneae Rchb.
 Mesechiteae Miers
 Echiteae Bartl.
PERIPLOCOIDEAE R. Br. ex Endl.
SECAMONOIDEAE Endl.
ASCLEPIADOIDEAE R. Br. ex Burnett
 Fockeeae Kunze, Meve & Liede
 Marsdenieae Benth.
 Ceropegieae Orb.
 Asclepiadeae (R. Br.) Duby

The first paper, by Potgieter and Albert (2001), probes the phylogenetic relationships of the Apocynaceae s.l., using plastid genome sequences of the *trn*L intron and *trn*L-F spacer. This represents the most comprehensive phylogenetic study of the Apocynaceae s.l. to date, including sequences for 152 accessions (75 Apocynaceae and 48 Asclepiadaceae), and representatives of all subfamilies and tribes recognized in Endress and Bruyns (2000). This work was undertaken mainly to address the lack of adequate sampling in earlier studies, especially with regard to the basalmost clades in the family. The results in most cases are similar to those in the previous studies by Sennblad and Bremer (1996, 2000), Sennblad et al. (1998), and Civeyrel et al. (1998), but provide better resolution, especially within the Rauvolfioideae, and for the placement of several genera, whose systematic position has been in dispute (e.g., *Haplophyton*, *Vallesia*, *Microplumeria*, *Laxoplumeria*). Surprises include the number of additional taxa at the very base of the tree, below *Alstonia*, which was the basalmost genus in the family in earlier analyses (Sennblad & Bremer, 1996, 2000; Endress et al., 1996; Civeyrel et al., 1998), demonstration of polyphyly of the Carisseae, Plumerieae, and Alyxieae sensu Leeuwenberg (1994), evidence for the multiple evolution of seed wings in various tribes of the Rau-

volfioideae, and support for the recognition of *Tonduzia*. The classification published by Endress and Bruyns (2000), and the large phylogenetic analysis of Apocynaceae s.l. by Potgieter and Albert (2001) published in this volume, did not take place in isolation but evolved through reciprocal exchange of information. In large part the classification of Endress and Bruyns (2000) was made more natural due to the inclusion of (at that time unpublished) results of the study by Potgieter and Albert (2001), generously provided by the authors.

The second paper, by Venter and Verhoeven (2001), focuses on the Periplocoideae. Although small in number of species (only 31 genera and 181 species), the poorly known Periplocoideae are at present the most enigmatic group of the Apocynaceae s.l. in terms of their systematic position. In terms of complexity they fall somewhere between the Apocynoideae and the Secamonoideae. Periplocoideae have always been the odd man out because their translator structure appears so different from that of the higher asclepiads, although there are actually more similarities in the translator structure of the two groups than may be apparent at first sight (Schick, 1982; Endress, in press). Their systematic position in the Apocynaceae s.l. remains uncertain: either they are the basal clade of the traditional Asclepiadaceae, or they form a clade separate from the Secamonoideae + Asclepiadoideae, but also nested in the higher Apocynoideae. In their paper Venter and Verhoeven (2001) provide an overview of the subfamily, including new synonymies and a key to the genera; a cladistic analysis based on morphological characters is also presented.

In the third paper, Verhoeven and Venter (2001) compare pollen morphology of Periplocoideae, Secamonoideae, and Asclepiadoideae. Traditionally, Periplocoideae were distinguished from Secamonoideae and Asclepiadoideae by having pollen in tetrads, whereas the other two subfamilies have pollinia. Recently, however, the authors have shown that some genera of Periplocoideae also have their pollen coalesced into pollinia (Verhoeven & Venter, 1998). In their current paper more taxa are added to the list. Each anther in Periplocoideae still has four pollen sacs (the ancestral state in the family) and thus in genera with pollinia, four pollinia are produced in each anther, as in Secamonoideae. This distinguishes Periplocoideae and Secamonoideae from the Asclepiadoideae, in which, during evolution, the two dorsal pollen sacs in the anther have been lost, so that each anther only produces two pollinia. The pollinia in Periplocoideae are also similar to those in Secamonoideae in that they are not covered by an outer pollinium wall, but are

composed merely of agglutinated tetrads. There are, however, differences between the two groups in the internal structure of the pollinia. Pollinia in Asclepiadoideae, in contrast, are composed of single grains, covered by an outer pollinium wall. The only exception known is *Fockea*, which has pollinia similar to those found in Secamonoideae and Periplocoideae. The unresolved position of Periplocoideae in Apocynaceae s.l. raises the question of whether pollinia have evolved independently in Periplocoideae and again in the Secamonoideae + Asclepiadoideae or whether they are homologous in these two groups. Results presented in this paper suggest that pollinia may have arisen twice within the Periplocoideae alone.

The fourth paper, by Civeyrel and Rowe (2001), explores phylogenetic relationships between and within the genera of Secamonoideae, as well as with other subfamilies, based on the plastid gene *mat*K. With only seven recognized genera and under 200 species, more than half of which belong to the genus *Secamone*, Secamonoideae are the smallest subfamily of Apocynaceae s.l. Like the Periplocoideae, the Secamonoideae are restricted to the Old World and are also poorly collected. Madagascar is the main center of speciation and contains half the known genera and species. Secamonoideae exhibit characteristics that are a mosaic of those from Asclepiadoideae on the one hand, and the more basal subfamilies of Apocynaceae s.l. on the other, and are thus one of the crucial groups in understanding the relationships within the family.

In the fifth paper, Fishbein (2001) plots various scenarios of diversification of two key characters in the former Asclepiadaceae, the pollinarium and the corona, onto a phylogenetic framework based on sequences of the plastid gene *mat*K. One of the most difficult tasks in the Apocynaceae s.l. is distinguishing homology from convergence. A major focus of continued dispute is the assessment of homology of various types of coronas. The analyses presented here suggest that evolution of pollinaria has been relatively conserved, whereas evolution of coronas, especially gynostegial coronas, which characterize the Asclepiadoideae, is marked by radiation and diversification. Since a gynostegial corona is taken to be the ancestral state in Asclepiadoideae, its absence in any taxa in this subfamily must be considered to be derived. In this study, independent loss of the corona is shown to have taken place twice within the Asclepiadeae alone, and other instances of loss are mentioned for this tribe. The findings are supported by those of Liede (2001). Based on the phylogenetic reconstruction presented here, it is most probable that pollinia in

the Periplocoideae have arisen independently from those in the higher asclepiads. In addition, there is support for two separate origins of pollinia within Periplocoideae, as proposed in Verhoeven and Venter's (2001) contribution.

The sixth paper, by Albers and Meve (2001), is a karyological survey of the traditional Asclepiadaceae, including chromosome numbers for 299 taxa published for the first time. The basic chromosome number of $x = 11$ was found in 96% of the taxa investigated, with no deviations from this number found in Periplocoideae or Secamonoideae. A general trend of decreasing size of karyotypes is described, with the largest karyotype lengths found in the basal groups and the smallest in the Asclepiadeae, which is presumed to be the most derived tribe in the Asclepiadoideae.

In the seventh paper, Liede (2001) assesses the subtribe Astephaninae (Asclepiadeae) based on *trn*T-L and *trn*L-F spacer and *trn*L intron sequences. The traditional delimitation of the tribe was based on the lack of a staminal corona. Twelve representatives of the Astephaninae, as traditionally circumscribed, were analyzed. The taxa were found to fall into two main clades. One of them, the Astephaninae clade, contains only the Old World genera *Astephanus* s. str., *Microloma*, and *Oncinema*. The New World taxa previously included in the genus *Astephanus*, in contrast, come out in the unrelated Metastelminae clade. The other main clade, the Tylophorinae clade, comprises seven former Astephaninae genera. This study shows that a corona has been lost at least twice within the taxa studied and underscores the danger of placing too much weight on any one character.

The papers presented here are a testimony to the progress made in our understanding of the phylogeny and evolution of the Apocynaceae s.l., but they also serve to highlight areas that are still most in need of further work. Foremost among these, at higher taxonomic levels, is the taxonomic position of the Periplocoideae. This subfamily is the key to determining whether or not the former Asclepiadaceae are monophyletic. Much work also remains to be done in elucidating phylogenetic relationships among the genera of the Periplocoideae. Molecular evidence would be a welcome addition to the morphological data available. Within the Rauvolfioideae and Apocynoideae the relationships among the tribes are still vague, and the placement and significance of taxa such as *Baissea* remain an enigma. Phylogenetic relationships between Apocynoideae of the Old World and those of the New World are uncharted waters. Within Asclepiadoideae, most work still remains to be done in Marsdenieae

and Asclepiadeae. In Marsdenieae, major difficulties still exist as to generic limits; in addition, the relationship of Marsdenieae and Ceropegieae remains uncertain. In the large tribe Asclepiadeae, much work remains to be done at all taxonomic levels: work on the composition and delimitation of subtribes is desirable, and there are large, presumably heterogeneous genera that need to be sorted out. For a student interested in working on the systematics of a fascinating group and not afraid of complexity, many opportunities await.

Literature Cited

Albers, F. & U. Meve. 2001. A karyological survey of Asclepiadoideae, Periplocoideae, and Secamonoideae, and evolutionary considerations within Apocynaceae s.l. Ann. Missouri Bot. Gard. 88: 624–656.

Civeyrel, L. & N. Rowe. 2001. Phylogenetic relationships of Secamonoideae based on the plastid gene matK, morphology, and biomechanics. Ann. Missouri Bot. Gard. 88: 583–602.

———, A. Le Thomas, K. Ferguson & M. Chase. 1998. Critical reexamination of palynological characters used to delimit Asclepiadaceae in comparison to the molecular phylogeny obtained from plastid matK sequences. Molec. Phylogenet. Evol. 9: 517–527.

Demeter, K. 1922. Vergleichende Asclepiadeenstudien. Flora 115: 130–176.

Endress, M. E. 2001. Apocynaceae and Asclepiadaceae: United they stand. Haseltonia 8: (in press).

——— & P. Bruyns. 2000. A revised classification of the Apocynaceae s.l. Bot. Rev. (Lancaster) 66: 1–56.

———, B. Sennblad, S. Nilsson, L. Civeyrel, M. Chase, S. Huysmans, E. Grafström & B. Bremer. 1996. A phylogenetic analysis of Apocynaceae s. str. and some related taxa in Gentianales: A multidisciplinary approach. Opera Bot. Belg. 7: 59–102.

Fishbein, M. 2001. Evolutionary innovation and diversification in the flowers of Asclepiadaceae. Ann. Missouri Bot. Gard. 88: 603–623.

Goyder, D. 1999. The Asclepiadaceae—A figment of our imagination? Pp. 309–317 in J. Timberlake & S. Kativu (editors), African Plants: Biodiversity, Taxonomy and Uses. Royal Botanic Gardens, Kew.

Judd, W. S., R. W. Sanders & M. J. Donoghue. 1994. Angiosperm family pairs: Preliminary phylogenetic analyses. Harvard Pap. Bot. 1(5): 1–51.

Jussieu, A. L. de. 1789. Genera Plantarum. Herissant, Paris.

Kunze, H., U. Meve & S. Liede. 1994. Cibirhiza albersiana, a new species of Asclepiadaceae, and establishment of the tribe Fockeeae. Taxon 43: 367–376.

Leeuwenberg, A. J. M. 1994. Taxa of the Apocynaceae above the genus level. Series of revisions of Apocynaceae, XXXVIII. Wageningen Agric. Univ. Pap. 94(3): 45–60.

Liede, S. 2001. Subtribe Astephaninae (Apocynaceae–Asclepiadoideae) reconsidered: New evidence based on cpDNA spacers. Ann. Missouri Bot. Gard. 88: 657–668.

——— & A. Täuber. 2000. Sarcostemma R. Br. (Apocynaceae–Asclepiadoideae)—A controversial generic circumscription reconsidered: Evidence from trnL-F spacers. Pl. Syst. Evol. 225: 133–140.

———, A. Täuber & J. Schneidt. Molecular considerations on the Tylophorinae K. Schum. (Apocynaceae–Asclepiadoideae). Edinburgh J. Bot. (in press).

Potgieter, K. & V. A. Albert. 2001. Phylogenetic relationships within Apocynaceae s.l. based on trnL intron and trnL-F spacer sequences and propagule characters. Ann. Missouri Bot. Gard. 88: 523–549.

Safwat, F. M. 1962. The floral morphology of Secamone and the evolution of the pollinating apparatus in Asclepiadaceae. Ann. Missouri Bot. Gard. 49: 95–129.

Schick, B. 1982. Zur Morphologie, Entwicklung, Feinstruktur und Funktion des Translators von Periploca L. (Asclepiadaceae). Trop. Subtrop. Pflanzenwelt 40: 513–553.

Schumann, K. 1895. Apocynaceae and Asclepiadaceae. In A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien 4(2): 109–306. Engelmann, Leipzig.

Sennblad, B. & B. Bremer. 1996. The familial and subfamilial relationships of Apocynaceae and Asclepiadaceae evaluated with rbcL data. Pl. Syst. Evol. 202: 153–175.

——— & ———. 2000. Is there a justification for differential a priori weighting in coding sequences? A case study from rbcL and Apocynaceae s.l. Syst. Biol. 49: 101–113.

———, M. E. Endress & B. Bremer. 1998. Morphology and molecular data in phylogenetic fraternity—The tribe Wrightieae (Apocynaceae) revisited. Amer. J. Bot. 85: 1143–1158.

Swarupanandan, K., J. K. Mangaly, T. K. Sonny, K. Kishorekumar & S. Chand Basha. 1996. The subfamilial and tribal classification of the family Asclepiadaceae. Bot. J. Linn. Soc. 120: 327–369.

Venter, H. J. T. & R. L. Verhoeven. 2001. Diversity and relationships within the Periplocoideae (Apocynaceae). Ann. Missouri Bot. Gard. 88: 550–568.

Verhoeven, R. L. & H. J. T. Venter. 1998. Pollinium structure in Periplocoideae (Apocynaceae). Grana 37: 1–14.

——— & ———. 2001. Pollen morphology of the Periplocoideae, Secamonoideae, and Asclepiadoideae (Apocynaceae). Ann. Missouri Bot. Gard. 88: 569–582.

Wanntorp, H.-E. 1988 [1989]. The genus Microloma (Asclepiadaceae). Opera Bot. 98: 1–69.

PHYLOGENETIC RELATIONSHIPS WITHIN APOCYNACEAE S.L. BASED ON *trn*L INTRON AND *trn*L-F SPACER SEQUENCES AND PROPAGULE CHARACTERS[1]

Kurt Potgieter[2] *and Victor A. Albert*[3]

Abstract

Relationships within Apocynaceae s.l. (Apocynaceae s. str., Periplocaceae, and Asclepiadaceae) were investigated by maximum parsimony analysis of morphological and molecular sequence data. Sequences of the plastid *trn*L intron and *trn*L-F spacer for 152 accessions for representatives of all major tribes were included in this study; 96% of these sequences represent new data. Two outgroups were selected from the closely related Loganiaceae. The total evidence matrix incorporated *trn*L intron and *trn*L-F spacer sequences, insertion/deletion information, and propagule characters. The phylogenetic hypothesis derived from this data set was used to evaluate the most current classification systems and was also used to investigate trends in seed dispersal. Apocynaceae s.l. are a strongly defined monophyletic group, a finding that should be reflected in taxonomic treatments. The recognition of three of the five subfamilies proposed by Endress and Bruyns in 2000 is supported by the monophyletic Periplocoideae, Secamonoideae, and Asclepiadoideae, whereas the paraphyletic Rauvolfioideae and Apocynoideae are not supported. The precise position of the Periplocoideae, however, remains unclear. Traditional tribal delimitations were less congruent with our total evidence phylogeny. The evolution of seed comas and enhanced long-distance dispersal within the Apocynaceae s.l. probably contributed to accelerated cladogenesis, ultimately giving rise to the majority of the extant genera within the family. Phylogeographic analysis of our data provides some evidence for a Gondwanan origin of the family.

Key words: Apocynaceae, Asclepiadaceae, Gentianales, Periplocaceae, *trn*L intron, *trn*L-F spacer.

The Apocynaceae Jussieu (1789) are a large and distinct clade of the Gentianales with nearly 4800 species distributed among 480 genera (Mabberley, 1997; Struwe et al., 1994, 1998). The above numbers represent Apocynaceae sensu lato, which includes the previously recognized families Asclepiadaceae and Periplocaceae (Demeter, 1922; Safwat, 1962; Stevens, 1975; Struwe et al., 1994; Judd et al., 1994; Thorne, 1992; Struwe et al., 1998; Civeyrel et al., 1998; Potgieter & Albert, 1997, 1998a,

b; Endress & Bruyns, 2000). The Asclepiadaceae and Periplocaceae represent clades showing parallel phylogenetic trends toward reproductive synorganization (Sennblad & Bremer, 1996; Civeyrel et al., 1998). Following the work of Brown (1810) and Schlechter (1905), the morphologically complex Asclepiadaceae and Periplocaceae have, until recently, been separately maintained. There has been recent interest in clarifying the phylogenetic relationships of the Apocynaceae, Asclepiadaceae,